PRIFYSGOL ABERYSTWYTH UNIVERSITY

Aberystwyth University

Soil biocrusts affect metabolic response to hydration on dunes in west Queensland, Australia

Thomas, Andrew D.; Elliott, David R.; Hardcastle, David; Strong, Craig L.; Bullard, Joanna; Webster, Richard; Lan, Shubin

Published in:
Geoderma

DOI:
10.1016/j.geoderma.2021.115464

Publication date:
2022

Citation for published version (APA):
Thomas, A. D., Elliott, D. R., Hardcastle, D., Strong, C. L., Bullard, J., Webster, R., & Lan, S. (2022). Soil biocrusts affect metabolic response to hydration on dunes in west Queensland, Australia. *Geoderma*, *405*, [115464]. https://doi.org/10.1016/j.geoderma.2021.115464

Document License
CC BY

General rights
Copyright and moral rights for the publications made accessible in the Aberystwyth Research Portal (the Institutional Repository) are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

• Users may download and print one copy of any publication from the Aberystwyth Research Portal for the purpose of private study or research.
• You may not further distribute the material or use it for any profit-making activity or commercial gain
• You may freely distribute the URL identifying the publication in the Aberystwyth Research Portal

Take down policy
If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

tel: +44 1970 62 2400
email: is@aber.ac.uk

Download date: 05. May. 2023

Geoderma 405 (2022) 115464

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Soil biocrusts affect metabolic response to hydration on dunes in west Queensland, Australia

Andrew D. Thomas [a,*], David R. Elliott [b], David Hardcastle [a], Craig L. Strong [c], Joanna Bullard [d], Richard Webster [e], Shubin Lan [a,f]

[a] Earth Surface Processes Research Group, Department of Geography and Earth Sciences, Aberystwyth University, Aberystwyth SY23 3DB, UK
[b] Environmental Sustainability Research Centre, University of Derby, DE11 1GB, UK
[c] Fenner School of Environment and Society, The Australian National University, Canberra, Australia
[d] Geography and Environment, Loughborough University, LE11 3TU, UK
[e] School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool L3 3AF, UK
[f] Key Laboratory of Algal Biology, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan 430072, China

ARTICLE INFO

Handling Editor: Matthew Tighe

Keywords:
Soil biocrusts
Drylands
Soil carbon
CO_2 flux
Photosynthesis
Hydration
Light

ABSTRACT

Soil biocrusts, formed from communities of microbes and their extracellular products are a common feature of dryland soil surfaces. Biocrust organisms are only intermittently metabolically active, but due to their ubiquity they make a significant contribution to the carbon cycle. Quantification of the controls and insights into the interlinked process of photosynthesis and respiration are essential to enhancing our understanding of the carbon cycle in the world's drylands. Yet, there have been relatively few field studies investigating controls on both biocrust photosynthesis and respiration. We undertook field-based experiments at two dune sites during the dry season in Diamantina National Park in Queensland, Australia to determine how biocrust hydration and illumination affect soil CO_2 flux and photosynthesis. Static chambers and an infra-red gas analyser were used to quantify soil CO_2 flux, and a fluorometer and a CFImager were used to determine a range of photosynthetic parameters in the field and laboratory respectively. When dry, biocrust photosynthetic activity was not detected and soil CO_2 flux was very low irrespective of biocrust cover. Hydration led to a large and immediate increase in CO_2 flux, which was more pronounced in the presence of biocrusts and on the dune with thinner biocrusts. Hydration also initiated the onset of photosynthesis in some biocrusts, which was greatest under low light conditions and sustained with further hydration. There were only infrequent periods of net CO_2 uptake to the soil, occurring when CO_2 uptake due to photosynthetic activity was less than background soil CO_2 flux. Chlorophyll fluorescence imaging indicated biocrust spatial heterogeneity was evident at the cm scale where microtopography creates a myriad of environments for different crust organisms. Our findings demonstrate that biocrusts are highly spatially heterogenetic at both landscape and small scale, which suggests the maintenance of biocrust spatial diversity is likely to be key to imparting resilience to changing climate and disturbance. As well as reaffirming the importance of biocrusts for the carbon cycle in dryland dune soils the study demonstrates that biocrust respiration and photosynthesis respond differently to hydration and shading. This adds an unpredictability to the distribution of soil carbon stocks and the gaseous exchanges of CO_2 between the surface and atmosphere. Future changes to precipitation and increased temperatures are likely to reduce soil moisture across much of the Australian interior and consequently biocrusts may experience a decline in biomass, structure, and function which could have significant repercussions beyond carbon stocks.

1. Introduction

The soil surface in drylands is an extreme environment that presents significant challenges to life. Soil surfaces are frequently desiccated, and experience only intermittent periods of hydration. In many dryland locations, annual temperature variations of > 70 °C and diurnal variations > 50 °C are common (Lembrechts et al., 2020) and levels of ultraviolet radiation can be very high (Pringault and Garcia-Pichel et al., 2004).

* Corresponding author.
E-mail address: ant23@aber.ac.uk (A.D. Thomas).

https://doi.org/10.1016/j.geoderma.2021.115464
Received 30 March 2021; Received in revised form 3 September 2021; Accepted 9 September 2021
Available online 21 September 2021
0016-7061/© 2021 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

These conditions constrain vascular plant cover and consequently vegetation is often found in a mosaic with extensive exposed soil patches (Ludwig et al., 2005). Soil surfaces are, however, home to a diverse community of microorganisms that form biocrusts. Soil biocrusts form from aggregates of mineral grains, microbes (especially cyanobacteria), lichen, mosses and extracellular polymeric substances (EPS) (Belnap et al., 2016). They are common in all drylands, including in Australia (Strong et al., 2013; Williams et al., 2014, Elliott et al., 2019). Biocrusts provide a range of important ecosystem functions (Ferrenberg et al., 2017), including fixing atmospheric nitrogen (Strauss et al., 2012) and improving soil stabilisation, which reduces the frequency and magnitude of soil erosion (Ravi et al., 2011). Autotrophic organisms in biocrusts can also photosynthesise and generate organic carbon, which consequently improves soil stability, water holding capacity and fertility (Grote et al., 2010; Coe et al., 2012). Despite being only intermittently metabolically active, biocrusts make a significant contribution to organic carbon stocks in drylands, sequestering *c.* 1.0 Pg C yr^{-1} globally (Elbert et al., 2012), and although soil organic carbon concentrations are low in drylands, their vast extent (*c.* 43% of the land surface) make them globally important.

The metabolic activity of biocrusts is affected by a range of biotic and abiotic factors (see for example, Johnson et al., 2012; Thomas et al., 2012; Wertin et al., 2012; Lane et al., 2013; Maestre et al., 2013). Biocrust organisms are poikilohydric, adapting passively to the available moisture around them (Tamm et al., 2018), and can withstand desiccation through metabolic dormancy (Lange et al., 1994). Hydration results in the rapid initiation of respiration followed by photosynthesis in biocrusts (Kranner and Birtić, 2005; Belnap et al., 2016). Although moisture and temperature are important factors in determining biocrust carbon balances (Lange et al., 1994; Tamm et al., 2018; Kranner and Birtić, 2005; Belnap et al., 2016), not all biocrust assemblages will respond to climatic variables in the same way; much will depend on microbial composition and how the dominant autotrophs react to the physiological stress associated with desiccation (Belnap et al., 2016). The effects are often subtle, and the timing of hydration may also be an important factor affecting the metabolic response to hydration. Williams et al. (2014) detected no photosynthetic activity or respiration after hydration of biocrusts in the dry season in northern Queensland. When the same biocrusts were hydrated in the wet season however, activity commenced almost immediately. They hypothesized that desiccated EPS protects cyanobacteria from premature resurrection in the dry season. Similar seasonal differences in carbon balance in response to identical hydration conditions have also been observed in moss-dominated crusts in North America (Coe et al., 2012). Biocrust photosynthetic efficiency can be inhibited by increased non-photochemical quenching and photoinhibition in conditions of high irradiance (García-Pichel and Belnap, 1996; Adir et al., 2003). Hence biocrust photosynthesis is most efficient in conditions of low irradiance typically found during cloudy conditions (Lan et al., 2014). Finally, biocrust carbon balances are also sensitive to disturbance. A two year field manipulation experiment on dunes in southern Botswana demonstrated that biocrust removal led to increases in soil CO_2 flux, and reductions in chlorophyll *a* and organic carbon, whereas light disturbance led to increases in chlorophyll *a* and organic carbon (Thomas, 2012).

Central Australia, along with many other dryland regions, is predicted to experience more frequent and longer periods of extreme heat in the future (Cowan et al., 2014; Huang et al., 2016) as well reductions in precipitation (IPCC, 2014). Consequently, soil moisture is likely to decrease in many areas (Bates et al., 2008) and biocrusts developed in these areas may experience a decline in biomass, structure, and function which could have significant repercussions on the regional and even global carbon stocks. Quantification of the controls and insights into the interlinked process of photosynthesis and respiration are therefore essential to enhancing our understanding of the carbon cycle in the world's drylands (see for example related work by Büdel et al., 2018; Dettweiler-Robinson et al., 2018). This study presents new information on how the presence of biocrusts in a dormant (desiccated) and active (hydrated) state affect the soil carbon balance of dune soils. The objectives were to quantify variability in the photosynthesis and respiration responses of dune surfaces in Australia with biocrusts and where they had been removed, and under varying hydration, temperature and light conditions, and to explore the variability in these responses at different scales. Our hypothesis is that respiration and photosynthesis will be greatest where there are biocrusts present on the dune surface, due to the presence of more autotrophic and heterotrophic microbial biomass (see for example Castillo-Monroy et al., 2011). We also expect hydration to greatly increase the autotropic and heterotrophic activity of the biocrusts, as is commonly reported elsewhere (e.g. Grote et al., 2010) and for low light conditions to favour metabolic activity. To test these hypotheses, we performed controlled experiments to determine the effects of biocrust removal, hydration, temperature and shading on soil CO_2 flux and photosynthesis on two sand dunes in Queensland, Australia.

2. Materials and methods

2.1. Study region

Field experiments were conducted in Diamantina National Park, western Queensland, Australia in July 2015 (Fig. 1). The 570 km^2 park takes its name from the Diamantina River, which flows south-west for 1000 km from the Swords Range to its terminus in Lake Eyre (Costelloe et al., 2003). The region is characterised by low relative relief, *c.* 100 m above sea level (Australian Height Datum), with anabranching river systems, expansive claypans, linear sand dunes and grassy downs interspersed across the region (Nanson and Knighton, 1996; Bullard et al., 2007). Dating of channel sediments in Cooper Creek, an adjacent catchment 200 km east of Diamantina, reveals there was a shift from sand-to-mud dominated channel transport around 40,000 years BP, which isolated the dunes as emergent features (Maroulis et al., (2007) and since then there has been very little dune movement. The park was formerly a pastoral holding, but by 1997 all grazing was prohibited (McTainsh and Strong, 2007), although the park continues to be impacted by illegal cattle grazing.

The region has a semi-arid climate, with extreme inter-annual temperature and rainfall regimes. The mean annual temperature is 24.7 °C but summer daytime temperatures can exceed 50 °C and winter night temperatures typically fall below 0 °C (Strong et al., 2013). Mean annual precipitation is 270 mm yr^{-1} (Chappell et al., 2007), with 75 % occurring between November and March during the Australian summer monsoon (Bullard et al., 2007; Strong et al., 2013). Data were collected in the dry season and after below average rainfall in the previous wet season year where there was only 110 mm precipitation (Chris Mitchell, Head Ranger, personal communication) was recorded at the Park Headquarters (Fig. 1).

2.2. Field sites

A field-based manipulative experiment was conducted on two linear dunes within the Park (Fig. 1). Both dunes were 2–3 km in length, 10–12 m high and comprised of very fine to fine sands with a modal particle-size of 185–270 μm. The pH of the upper 5 cm of dune sand was 6.4. The first study dune, named T1D after the dominant biocrust cover, was located 5.5 km south-east of the National Park Headquarters on the east bank of the Diamantina River (23° 48′ 29′′ S, 141° 09′ 34′′ E). Vegetation covered approximately 25 % of the ground surface, with Golden Wattle (*Acacia pycnantha*), Saltbush (*Atriplex spongiosa*) and Broom Bush (*Viminaria juncea*) dominant on the dune and Coolabah trees (*Eucalyptus coolabah*) marking the high line of floodwaters at the base of the dune. Soil biocrusts covered 50 – 60 % of the open ground on the dunes, higher than the 35 % previously reported by Strong et al. (2013) for the wider Diamantina landscape. All biocrusts were light coloured, 3–4 mm thick

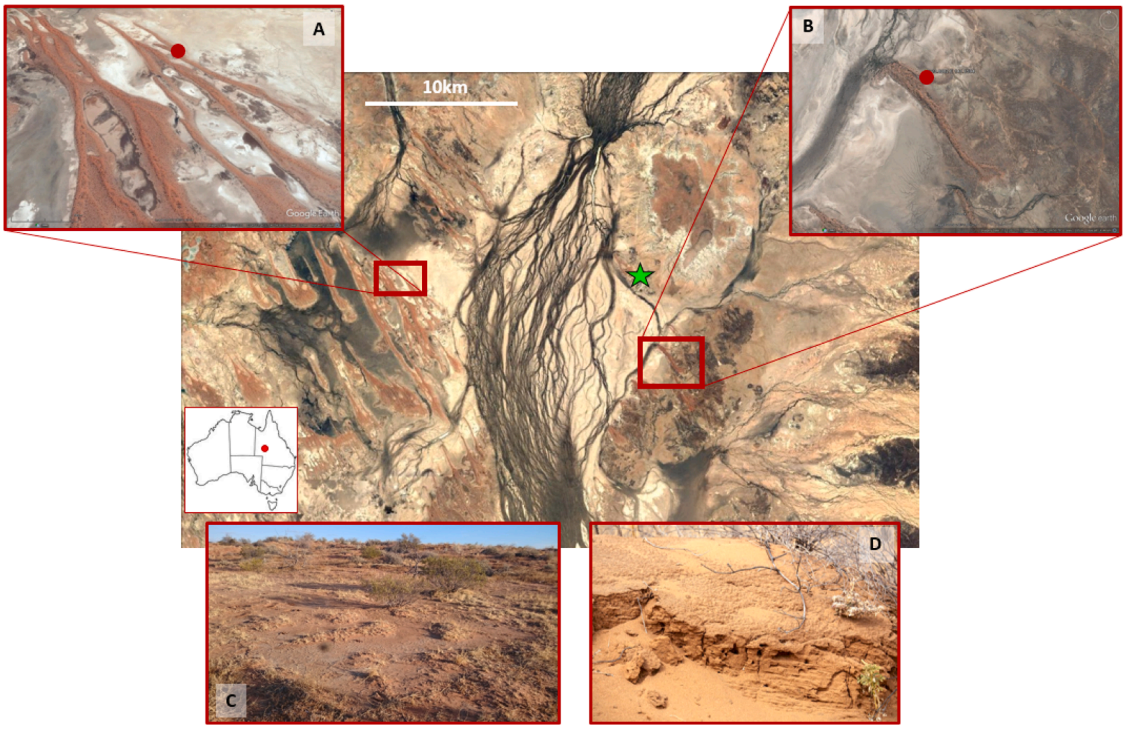

Fig. 1. Location of study sites in Diamantina National Park, Queensland, Australia. A) T2D, B) T1D, C) Biocrust covered dune surface at T1D, D) Cross-section through dune surface showing buried biocrust layers at T2D. Green star shows the location of the Park Headquarters. Main image and images A and B from Google Earth.

(Fig. 1) and were comparable to the light cyanobacterial or "type 1" biocrusts described in Thomas and Dougill (2006) from the Kalahari and in Strong et al. (2013) at other sites within the Diamantina National Park. There was evidence of biocrust disturbance due to cattle incursions and wind-scour across the site.

The second dune, named T2D after the better developed thicker biocrusts found at the site, was 15 km west of the Park Headquarters on the west bank of the Diamantina (23° 46′ 11′' S, 140° 59′ 50′' E) (Fig. 1). Vegetation cover at this site was approximately 30 %, with the same dominant species as T1D. There was no evidence of cattle disturbance, and biocrusts covered 50 – 60 % of the ground surface and were thicker (*c.* 5 mm) with some darker patches and notable microtopography. The biocrusts at this site are comparable to the "type 2" crusts described in Thomas and Dougill (2006) from the Kalahari and in Strong et al. (2013) from nearby sites in Diamantina. DNA sequencing confirms earlier microscopy work by Strong et al. (2013) that the dominant autotrophs in the biocrusts at T2D were cyanobacteria of the genus *Microcoleus,* which accounted for over 8 % of bacterial sequences detected (Elliott et al., 2019).

2.3. Soil properties

Bulk density was determined at five locations on each dune after weighing the oven dry mass of soil collected from 10 cm depth using a stainless steel tube with an internal volume of 99 cm^3. Further samples were collected from the biocrust and from 2 to 5 cm, 5–10 cm, 20–25 cm, 35–40 cm and 50–55 cm in a soil pit on each dune. Porosity was determined by calculating the volume of water needed to saturate a known volume of sand. Grain density was then derived by dividing the oven dry sample mass by the volume taken up by the solid grains. A further 18 and 10 replicate samples were collected from biocrusts and from 2 to 5 cm depth at T1D and T2D respectively and an elemental analyser (vario PYRO cube, Elementar UK Ltd.) was used to determine the total C and total N content of *c.* 30 mg sub-samples in tin capsules.

2.4. Soil CO_2 flux and the effect of biocrusts and hydration

On each dune, 18 static soil CO_2 flux chambers (Thomas et al., 2018) were installed across a 200 m long section of NE-facing mid-dune flank. Measurements were taken three or four times each day to determine CO_2 flux at a range of temperature and light conditions. The chambers were made from white uPVC and comprised two parts: A lower chamber (10.4 cm internal diameter and 12 cm height) that when pushed several cm into the surface forms an air-tight seal; and a screw on lid that enables gas to accumulate inside the chamber during measurement cycles. Chambers enclosed 85 cm^2 of soil and ranged from 480 – 570 mL in volume depending on insertion depth. Heat sinks mounted through the chamber walls ensured the internal air temperature were not elevated above ambient. The chamber lids include a port covered with a Suba seal for gas extraction and a vent valve to ensure any pressure differences were rapidly equilibrated. A 7 cm diameter borosilicate glass window in the centre of the lid permitted solar illumination of the soil surface throughout the entire PAR spectrum.

Immediately prior to gas sampling, soil surface temperatures were recorded at three points inside the chamber using an infra-red thermometer and the moisture content of the soil determined adjacent to the chamber by vertically inserting a SM150 soil moisture probe into the uppermost 10 cm soil (Delta-T Devices Ltd., Cambridge, UK). The lid was placed on the chamber and 12 mL of gas was immediately extracted through the sample port using a syringe and hypodermic needle secured with a luer lock. After approximately five minutes, another syringe was used to gently pump and mix the air within the chamber before a second sample was collected and the lids removed. CO_2 concentrations were determined immediately after each measurement cycle using an EGM-4 infrared gas analyser (PP Systems, Amesbury, USA). Mass CO_2 flux in mg m^{-2} hr^{-1}, normalised to mean temperature and pressure was determined using Equation 1 (Kutzbach et al., 2007):

$$CO_2flux = \frac{(C_2 - C_1)}{Tn} * \frac{V}{A} * T_f$$

where C_1 and C_2 are the initial and final CO_2 concentrations; T is the time between the first and final CO_2 samples; V is the volume of air inside above soil inside the chamber; A is the area of soil enclosed by the chamber; and T_f = a temperature factor. To correct for the effect of any diffusion suppression owing to the accumulation of CO_2 inside the chamber, a correction factor was applied (for details see Thomas, 2012). Chamber air temperatures and relative humidity were logged at 10 min intervals by USB502 loggers (Adept Science, UK) in six of the chambers. Soil volumetric water content and temperature were also determined every 10 min using a Decagon EM4 logger and four 5TM sensors inserted laterally into the soil at 2 cm, 5 cm, 10 cm and 20 cm in a soil pit located in the centre of the dune flank.

Each chamber location was assigned one of four treatments: i) crusted; ii) crust removed; iii) crusted and hydrated; iv) crust removed and hydrated. Dry treatments were replicated 4 times and hydrated treatments 5 times. Treatments were allocated to chambers based on their mean CO_2 flux over a 2 day period before any treatments were applied, such that there was an even distribution of treatment types across the full range of control CO_2 flux values. Any spatial clusters were addressed by reassigning treatments where necessary. This method helps prevent pre-existing (and undocumented) gradients or factors from obscuring the real effects of treatments or from generating spurious ones (Hurlbert, 1984). For the crust-removed treatments, the chamber was removed, and a spatula was used to lift all consolidated crust material from the soil. The chamber was then carefully replaced in the same location and the chamber head space volume recalculated. Boiled rainwater collected from a tank at the ranger station was used for the hydration treatments. An initial 15 mm equivalent was applied to the soil surface within and surrounding the respiration chamber and an additional 5 mm was applied 2 days later. The same depth of water was also applied to a 1 m^2 area of soil above the 5TM buried soil temperature and moisture sensors. The amount of water applied for the hydration treatments reflects the rainfall regime (Bullard et al. 2018) of the region where up to 80% of annual rainfall occurs during multi-day events and over 75 % of rainfall amounts recorded on one day are < 6 mm. It is important to note that the sites are in a summer rainfall region and the experiments were done in the winter. A total of 360 soil CO_2 flux measurements were taken on each dune over 12 days (20 times per chamber over the pre- and post-treatment phases).

2.5. Field measurements of biocrust photosynthetic activity

A portable fluorometer (FluorPen FP 100, PSI systems, Czech Republic) using a 650 nm wavelength, was used to determine quantum yield in the field. Quantum yield is the most commonly used parameter in assessing the efficiency of photosystem II. Two values, Fv/Fm and Fv'/Fm', were obtained for dark and light adapted biocrusts respectively (where Fm is the fluorescence maximum; Fv is equal to Fm – Fo, and Fo is the fluorescence origin). The fluorometer was also used to generate light curves, using pulse modulate fluorometry, where seven light phases, each 60 s duration, at 10, 20, 50, 100, 300, 500 and 1000 μmol m^2 s^{-1} intensity were used to determine the most effective quantum yield of photosynthesis under increasing light intensities throughout continuous illumination. Determination of quantum yield is rapid, taking approximately 15 s, whereas light curve responses take 15 min.

Intact biocrusts were collected from 16 locations on each dune using sterile Petri dishes (47 mm diameter × 18 mm deep). The samples were arranged on a bench close to the dune from where they originated. Modified leaf clips (Hansatech Instruments Ltd, Norfolk, UK) originally intended for measuring leaf fluorescence, were then attached to each Petri dish. These provided a 4 mm diameter opening for crust illumination and an in-built shutter cover to allow dark adaptation (when required for the dark adapted fluorescence protocol). The FluorPen was held with a retort stand and blackout material was wrapped around the sample and sensor during measurements to ensure all light was prevented from reaching the samples. The quantum yield and light curve measurement protocols were then followed to quantify biocrust photosynthetic activity (FluorPen FP 100 series Manual; Misra et al. 2012). During the measurements the amount of photosynthetically active radiation (PAR) reaching the samples from natural daylight illumination was logged continually using a Decagon EM4 logger and QSO-S sensor. First and last light was approximately 07:15 and 18:10 respectively, with solar noon and maximum PAR at 12:30. Maximum daily air temperatures were recorded at 14:30 and minimum temperatures at 06:00.

Photosynthesis parameters were monitored for one day prior to the application of one of four different treatments for each of the 16 samples (replication level of 4 per treatment) as follows: i) unshaded dry (dormant), ii) unshaded and hydrated (active), iii) shaded dry (dormant), and iv) shaded and hydrated (active). For the hydration treatments, 3.8 g of water (1 mm equivalent) was added to each sample every two hours and left for 20 min prior to undertaking the fluorescence measurements. There were five hydration/measurement cycles each day at 09:00, 11:00, 13:00, 15:00, and 17:30 to ensure measurements were made over a range of solar radiation and temperature conditions and so that the effects of cumulative hydration could be determined. Measurements were made in a randomised block order, to ensure there was no temporal bias, which was particularly important for hydrated samples. For the shaded treatments, shade netting was used to reduce the intensity of light reaching the biocrust samples. A portable spectrophotometer was used to confirm that the effect of the netting was to reduce UV (290–400 nm) and PAR (400–700 nm) by 43 to 45 %. For dark-adapted measurement protocols, the modified leaf clips were closed to prevent light reaching the samples. After 30 min the samples were placed under blackout material so the clips could be opened prior to the measurements being taken with the FluorPen.

2.6. Laboratory measurements of biocrust photosynthetic activity

The samples collected for *in-situ* determination of photosynthetic activity were returned to the UK in sealed Petri-dishes for further investigation of the small scale spatial heterogeneity of photosynthetic activity and how this is affected by hydration. Two biocrust samples from T2D were hydrated with 3 mL distilled water for 24 h prior to the experiment, whilst a further two samples were left air dry. Light adapted fluorescence maximum (Fm') values were then determined using a Technologica CFImager (Technologica, UK). All samples were hydrated immediately prior to the start of imaging using 1 mL of distilled water, then three more times (2 mL) throughout the 28-hour run time; samples were imaged every 30 min and kept under light at 400 μmol m^{-2} s^{-1} PAR.

2.7. Statistical analyses

All statistical analyses were performed using SPSS (IBM v. 25). One-way analysis of variance (ANOVA) was used to test the hypothesis that mean values of moisture, bulk density, total C, total N were significantly different between dunes. To test the significance of any differences in CO_2 flux and quantum yield between dunes and between treatments within each dune where multiple readings at were taken over the duration of the experiment, repeated measures ANOVA tests were conducted. The Levene's F statistic was used to test equality of variance and although ANOVA can tolerate inhomogeneous variance, where these conditions were not met the more robust Welch and Brown Forsythe tests of significance were used. Tukey's HSD post-hoc test was undertaken to determine which properties were significantly different due to treatment with a probability of $p < 0.05$.

3. Results

3.1. Soil properties

The mean moisture content of untreated biocrusts and soils were low (<0.27 vol%) and not significantly different between dunes ($p > 0.05$) (Table 1). Soils at T2D were significantly more porous than at T1D ($p = 0.02$, $df = 1$, $f = 6.80$). Bulk density varied with depth at both sites from 1.43 to 1.61 g cm^{-3} (Table 1). Total N and total C concentrations were low at both sites (<0.1 %) with greater concentrations in biocrusts compared to the underlying soil (Table 2). Soil C:N ratios range from 1 to 3 and are very low for dryland soils.

3.2. Soil CO_2 flux in relation to hydration and presence of biocrust

Pre-treatment mean soil CO_2 flux was significantly greater at T1D (15.9 – 17.5 mg CO_2 m^{-2} hr^{-1}) and more variable compared to T2D (10.0 – 11.4 mg CO_2 m^{-2} hr^{-1}) ($p = 0.01$, $df = 1$, $f = 27.58$) (Table 3). Positive flux values are indicative of a net CO_2 release from the soil to the atmosphere, whereas negative values indicative a net uptake of CO_2 to the soil. At both sites, removing the crust on dry and hydrated soils had no significant effect on CO_2 flux. CO_2 flux was significantly greater from the hydrated sites compared to the other sites at T1D ($p = <0.01$, $df = 3$, $f = 15.74$) and at T2D ($p = <0.01$, $df = 3$, $f = 8.25$). In dry conditions, crust removal decreased the spatial variability of CO_2 flux whereas hydration led to a significant increase in the spatial variability of flux at both dunes (Table 3b).

A more detailed insight into the effect of crusts and hydration on soil CO_2 flux can be seen in Table 3. At T1D the 15 mm hydration treatment led to a 12-fold increase in flux at sites where the crust was intact and a 6-fold increase where it had been removed (Table 3). The response to the subsequent 5 mm hydration was muted in comparison, with only small increases in flux, which again, were slightly larger at the crusted plots compared to the non-crusted plots. The elevated fluxes persisted at both sets of plots for the duration of the experiment and were significantly higher at the crusted compared to the non-crusted plots. At T2D the initial hydration treatment led to a *c*. 10-fold increase in CO_2 flux at sites where the crust was left intact and a 6-fold increase where it had been removed. The application of a further 5 mm rainfall had an insignificant effect on flux. After hydration, flux was not significantly different to pre-treatment conditions (Table 3).

Despite the wide range of values (2 – 40 °C), soil temperature alone was a very poor predictor of soil CO_2 flux at both sites (Fig. 2). Crust removal and hydration also made little difference to the relationship between CO_2 flux and soil temperature. Fig. 2 also demonstrates that occasionally there was negative flux (where CO_2 concentrations decline over time inside the chamber, indicative of a net uptake of CO_2 to the soil), and these instances occurred across a range of temperatures and treatments.

Table 1
Moisture, bulk density, porosity and grain density soil profiles at T1D and T2D. Means with standard deviations. Single values only below the surface, n = 5 for surface data. n.d. = no data.

Depth (cm)	Moisture (Vol. %)		Bulk Density (g cm^{-3})		Porosity (%)		Grain density (g cm^{-3})	
	T1D	T2D	T1D	T2D	T1D	T2D	T1D	T2D
Surface	0.18 ± 0.03	0.27 ± 0.15	1.55 ± 0.04	1.53 ± 0.04	36.0 ± 0.6	37.5 ± 1.5	2.43 ± 0.08	2.45 ± 0.06
2–5 cm	0.26	0.29	1.56	1.59	34.5	37.3	2.38	2.53
5–10 cm	0.29	0.41	1.55	1.61	36.1	38.4	2.42	2.61
20–25 cm	0.30	n.d.	1.52	n.d.	36.1	37.8	2.38	n.d.
35–40 cm	0.29	0.69	1.47	1.45	34.4	37.3	2.24	2.31
50–55 cm	0.44	0.83	1.51	1.43	35.8	37.0	2.35	2.27

Table 2
Mean ± standard deviation of total N and total C (%) concentrations from biocrusts and subsurface sediment from T1D and T2D. n = 18 for all samples from T1D, n = 10 from T2D samples.

Location	Biocrust		Subsoil	
	Total N (%)	**Total C (%)**	**Total N (%)**	**Total C (%)**
T1D	0.03 ± 0.01	0.07 ± 0.04	0.02 ± 0.01	0.05 ± 0.04
T2D	0.03 ± 0.001	0.10 ± 0.09	0.02 ± 0.01	0.02 ± 0.01

Table 3
CO_2 flux (mg CO_2 m^{-2} hr^{-1}) as a response to hydration treatments on crusted and crust removed locations on T1D and T2D. CO_2 flux reported as the mean ± standard deviation of all chambers over the treatment period. The variability in CO_2 flux between chambers (spatial variance) on each dune is quantified as the coefficient of variation (CV) (%) in the pre- and post- hydration phases.

	T1D		T2D	
	With Crust	Crust Removed	With Crust	Crust Removed
Before hydration	17.5 ± 6.6	15.9 ± 6.3	11.4 ± 6.4	10.0 ± 4.7
Immediately after 1st hydration	207.8 ± 83.8	92.4 ± 37.1	115.4 ± 26.5	61.9 ± 24.4
Immediately after 2nd hydration	52.4 ± 16.6	30.3 ± 12.3	10.1 ± 11.1	11.5 ± 9.6
Longer-term post hydration	31.5 ± 22.3	17.7 ± 12.2	12.8 ± 6.1	11.7 ± 4.7
CV before hydration	34.7	25.0	47.3	26.5
CV after hydration	60.7	110.1	136.7	95.1

3.3. Biocrust photosynthesis

No photosynthetic activity was detected in any sample from either site prior to hydration. Following hydration photosynthetic activity was detected in all samples from T2D, but not in any samples from T1D. The mean daily light adapted quantum yield of hydrated shaded and unshaded biocrusts (Table 4) from T2D are shown in Fig. 3. The quantum yield of the shaded biocrust was significantly higher than the unshaded on days 2, 3, and 5 ($p = 0.037$, 0.023, and 0.05 respectively). Generally, the biocrust quantum yield increases through time after repeated hydration with a significant ($p = <0.001$) increase in photosynthetic activity throughout the four days for shaded and unshaded samples (Fig. 3). The effect of light intensity can be seen in Fig. 4, where a decline in quantum yield as light intensity increases is also apparent for both shaded and unshaded treatments. Initially, shaded biocrusts produce a higher yield than unshaded. However, they demonstrate a steeper decline with increasing light intensity and for light levels of 300 μmol m^{-2} s^{-1} and above there is no significant difference between the two treatments.

3.4. Chlorophyll fluorescence imaging: CFImager

The fluorescence images clearly show the photosynthetic response to moisture, with photosynthetic activity initiating rapidly following hydration and continuing until the samples are dry (Fig. 5). Most activity was detected after 1 h and 15 mins and slowly declined thereafter. The images also highlight the considerable small-scale spatial heterogeneity of the photosynthetic activity and its response to the hydration process.

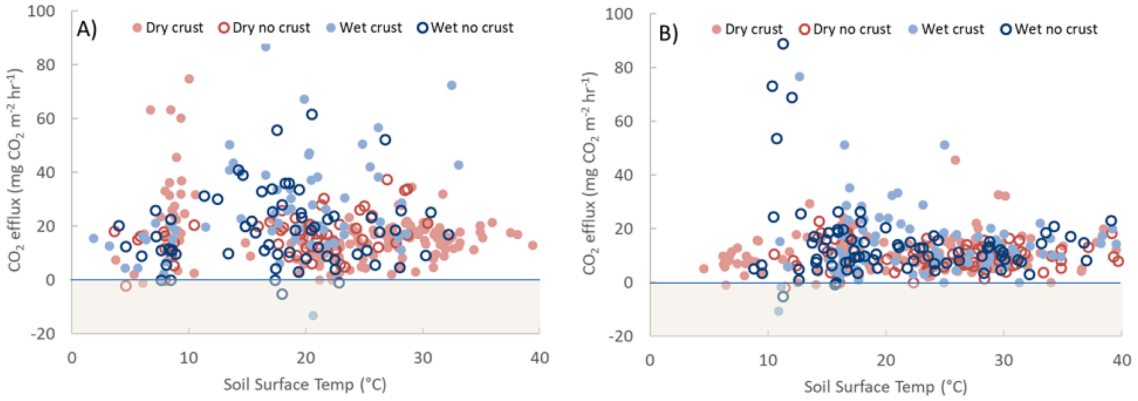

Fig. 2. Soil CO_2 flux (mg CO_2 m^{-2} hr^{-1}) and soil surface temperatures from treated and untreated plots at A) T1D and B) T2D. Fluxes during in the first measurement after hydration are not included. Shaded area covers negative flux values where the is a net sequestration of CO_2 to the soil.

Table 4
Photosynthetically active radiation (PAR), air temperatures in shaded and unshaded conditions and mean soil surface temperatures over the duration of the field data collection.

	T1D	T2D
Max. / min. unshaded air temperature (°C)	39 / −3.0	46.5 / 1.0
Max. / min. shaded air temperature (°C)	32.5 / −3.0	42.5 / 1.0
Mean soil surface temperature (°C)	16.4 ± 11.3	20.8 ± 11.1
Unshaded peak PAR (μmol m^{-2} s^{-1})	1611	1540
Shaded peak PAR (μmol m^{-2} s^{-1})	886	878

4. Discussion

4.1. Biocrusts and CO_2 flux

Soil CO_2 flux under desiccated conditions was, as expected, very low irrespective of biocrust cover, and comparable to other dryland locations in the dry season (see for example, Thomas et al., 2018). Most CO_2 likely originated from subsoil heterotrophic microorganisms and vascular plants roots able to access greater soil moisture at depth (Table 1). Moisture was the dominant control on soil metabolic activity, with artificial hydration leading to a large and immediate increase in CO_2 flux (Table 3). In contrast, there was no clear relationship between CO_2 flux and soil temperatures under any treatment (Fig. 2). The presence of biocrusts increased the soil respiration response to hydration at both sites but the thinner, less developed biocrusts at T1D responded to hydration with a greater increase in CO_2 flux than at T2D (Table 3). The apparently contradictory finding of the thicker, better developed biocrusts resulting in lower CO_2 flux at T2D can be explained by photosynthetic activity (or other processes) resulting in a reduction in net CO_2 emissions due to simultaneous CO_2 uptake (see below).

The increase in respired CO_2 after hydration of dry biocrusts has been observed elsewhere, including in the southwest Kalahari where soil respiration, remained 5–6 times greater than the very low background levels for at least 2 days after artificial wetting (Thomas and Hoon, 2010). Soil water potentials in dryland soils can fall below −20 MPa (Kieft et al., 1987) placing soil organisms under significant physiological stress. A rapid increase in soil water revives soil microorganisms from dormancy but osmotic shock causes a different type of stress (Placella et al., 2012) and even widespread microbial mortality (Birch 1964). The associated flush of available carbon associated with rapid hydration is a hugely significant characteristic of dryland ecology and soils (Fierer and Schimel 2002, Miller et al., 2005; Slate et al. 2019). The magnitude and speed of the hydration response from the crusted soils demonstrates the importance of post-rainfall CO_2 flux to the total net carbon exchange at the site and in drylands in general. Hydration levels in this experiment were designed to activate the uppermost soil layers and/or biocrust and will not have affected the water available to deeper rooting plants or microorganisms. The experiment therefore clearly demonstrates that

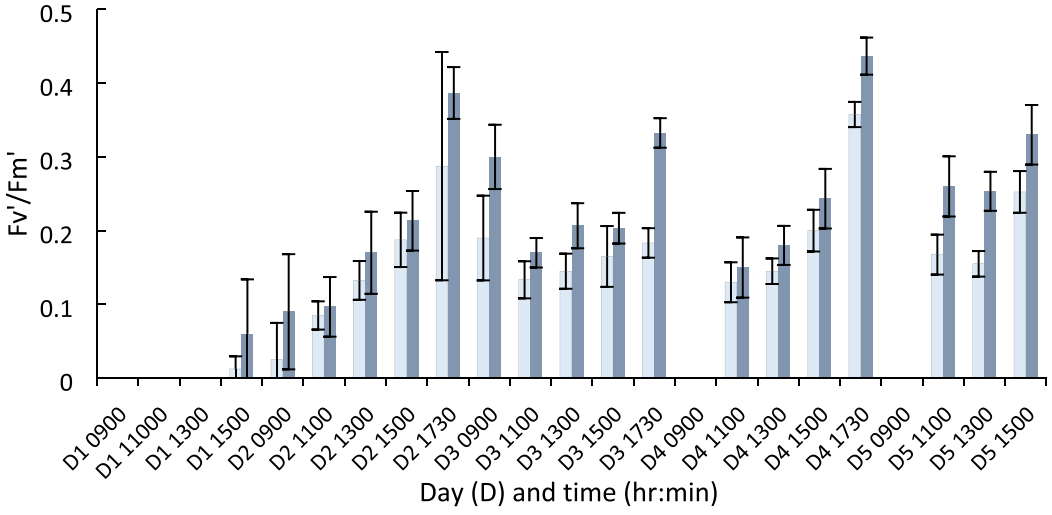

Fig. 3. Mean quantum yield (with standard deviation) of hydrated shaded (darker bars) and hydrated unshaded (lighter bars) biocrust samples from T2D. Sample n = 4 and 3 respectively.

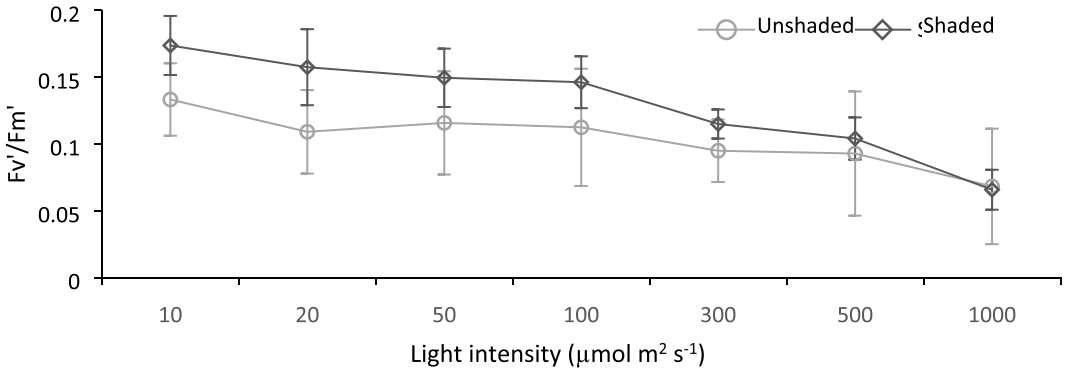

Fig. 4. Photosynthetic response of T2D biocrusts to increasing light intensities. Mean values of all hydrated measures ± standard deviation, n = 9 for both treatments.

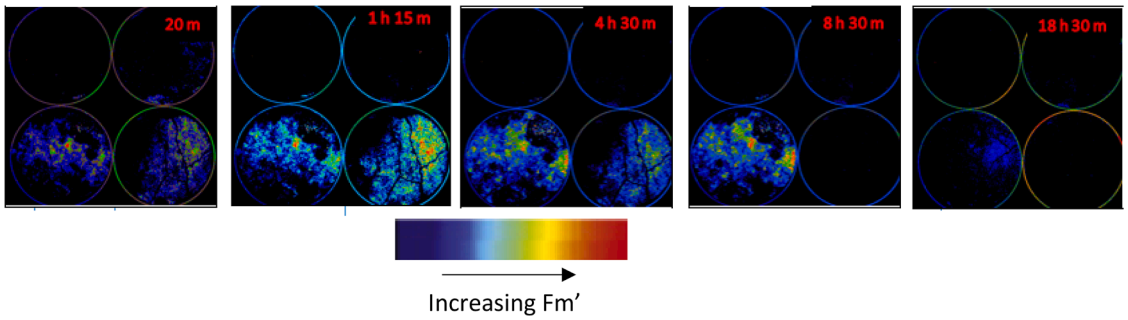

Fig. 5. Chlorophyll fluorescence images showing T2D biocrust photosynthetic activity in response to hydration and desiccation. Top two samples are dry; while bottom two were hydrated for 24 h prior to the determination. Dark colours (black/blue) represent low fluorescence, with bright (orange/red) indicating high photosynthetic activity. Time unit (red) represents how long has elapsed since the most recent hydration.

biocrusts are vital to this process, as without them, the response is either muted or not observed (Table 3).

Soil CO_2 flux may also be affected by the multiple buried crusted layers (Fig. 1, image D) that will create a complex stratigraphy of changing gas diffusivity in seemingly uniform sand soil profiles (Felde et al., 2018). Although soils were more porous at T2D, and therefore may facilitate greater rainfall infiltration depths and gas movement, there is no evidence that this resulted in greater background CO_2 emissions from the subsoil. Vertical variation in soil physical properties may, however, lead to stratification of microorganisms in response to micro-environmental gradients and affect biocrust response to moisture temperature and light (Lan et al., 2012; Hu et al., 2003; Garcia-Pichel and Belnap, 1996).

There were infrequent occasions at both sites where net CO_2 uptake to the soil was observed (Fig. 2). The two largest uptake values were on hydrated crusted soils, but it also occurred on hydrated soil where the biocrust had been removed. This could be due to water stimulating photosynthesis and CO_2 sequestration at a rate greater than background levels of respiration, leading to net uptake. Heterotrophic CO_2 fixation is known to occur in soils and is likely to be a widespread phenomenon (e.g. Miltner et al., 2005; Šantrůčková et al., 2005). Fixation is also enhanced by the availability of substrates and therefore be closely linked to respiration of aerobic heterotrophic microorganisms (Miltner et al., 2005). If this is a biological process, then the reason for net uptake occurring at locations where biocrusts had been removed is likely due to the presence of autotrophic organisms remaining in the soil immediately below the biocrust. It is worth noting that rates of photosynthetic activity or chemical CO_2 uptake could be occurring at levels below that of background soil CO_2 flux and will therefore not be recorded as net CO_2 uptake. In either case, the reason for the intermittent occurrence of the CO_2 uptake phenomena is uncertain and it is something worthy of future investigation.

4.2. *Biocrusts and photosynthetic activity*

No photosynthetic activity was detected at any sites without prior activation of biocrusts with additional moisture. At T2D, photosynthetic activity was detected in biocrusts after hydration (Figs. 3, 4). Previous laboratory work on crusts from Diamantina reported a similarly rapid photosynthetic response of biocrusts to hydration (Strong et al., 2013), with around 14 % moisture (or 1.5 mm rainfall equivalent) needed to sustain activity. As well as hydration, this earlier work clearly showed the controlling influence of nutrient content on photosynthetic yield. Our data also show that sustained hydration is also beneficial for photosynthesis (Fig. 3). It is likely that after the first rainfall when cyanobacteria have been reactivated, they will enter 'less dormant' state upon drying. They are then primed to resume photosynthesis and can do so with an enhanced rate, as they have more available ATP and nitrogenase (Belnap, 2003).

In contrast, no photosynthetic activity was detected in biocrusts at T1D even after hydration and despite their greater CO_2 flux response to hydration (Table 3). There are several reasons why this may have occurred. It is possible that motile cyanobacteria were active but located too deep in the crust to detect. The PSI Fluorpen used in this study will only detect fluorescence emitted from the surface. However, as less than 1% of PAR can penetrate deeper than 1 mm and cyanobacteria have not been found to photosynthesise at depths beyond 5 mm (García-Pichel and Belnap, 1996), it is unlikely that they were active but not detectable. We must stress, however, that these are hypotheses and further investigation is needed to determine the reasons for the contrasting responses

on each dune. What is clear is that photosynthesis and carbon uptake in biocrusts is complex and dependent on a variety of factors including hydration, composition, and shading. Climatic or environmental changes which favour one strategy over the other may alter the spatial distribution and microbial composition of biocrusts with implications for photosynthesis and carbon uptake. This is important because the distinctive biocrusts will respond differently to future changes to water availability, creating a more fragmented mosaic of soil properties with significant implications for the carbon cycle.

Biocrust photosynthetic activity was inversely related to light intensity and quantum yield was greater in shaded biocrusts that unshaded (Fig. 3). Differences in quantum yield between the unshaded and shaded biocrusts decreased with light intensity. This suggests that biocrust photosynthesis is most efficient at lower light intensities. These findings support a growing body of research which also shows that a reduction in light intensity, in particular UV radiation, is preferable for biocrust photosynthesis (e.g. García-Pichel and Belnap, 1996; Adir et al., 2003, Tracy et al., 2010, Lan et al., 2019). However, biocrust cyanobacteria can be resistant to photoinhibition, a trait important in their ability to resume photosynthesis immediately upon re-wetting (Harel et al., 2004), often under high light intensities, such as that found at 13:00 in Fig. 4.

Biocrust spatial heterogeneity is also evident at the cm scale, where microtopography likely creates a myriad of environments with different temperature, light and moisture conditions for different crust organisms (Fig. 5). At small scales, including within patches of biocrust (i.e. sub cm) the controls on and implications of biocrust heterogeneity remain poorly understood. Lan et al. (2019) found that distribution patterns of chlorophyll fluorescence varied at different spatial scales and among different crust types in the Tengger Desert, China. Our data also show that there is small-scale heterogeneity in biocrust photosynthetic activity which varies according to the hydration state. This small-scale variation may be related to microtopography, which provides cooler, shaded micro-sites that maintain suitable conditions for microorganism metabolic activity for longer than less shaded spots. The data also have implications for field sampling design, highlighting the importance of taking multiple measurements at different scales to capture the range of biocrust conditions and responses.

4.3. Wider implications

Our study has shown that undisturbed and well-developed biocrusts that have a strong respiration response to hydration may not produce a detectable photosynthetic response, even after sustained hydration. Soils, even in close proximity, can have subtle differences in biocrust cover and characteristics, that will affect soil carbon stocks and fluxes. Controls on the distribution and characteristics of biocrust at the regional scale include temperature, precipitation and soil properties (including pH, grain size, nutrients (Viles, 2008)). At smaller scales, grazing intensity and vegetation cover are more important (e.g. Berkeley et al., 2005; Thomas, 2012) and are likely reasons for differences in Diamantina. Site history and proximity to sources of microbial inoculum may be an additional reason for differences in biocrust type and soil functionality on the two dunes in this study. Rare river flood events are critical in depositing fresh sediment and microbes onto the claypans. Upon desiccation this material is readily deflated and redistributed throughout the landscape, including on the dunes (Elliott et al., 2019). However, Elliott et al. (2019) demonstrated that biocrust taxa from Diamantina vary in their capacity to be mobilised by the wind, hence the distribution of biocrust taxa in the dunes is a combined function of abiotic and biotic factors. Our findings demonstrate that there can be contrasting biocrust types and metabolic activity on similar dunes in close proximity. There is still much to learn about the relationship between the diversity of biocrust communities and how their metabolic characteristics respond to climatic variables and disturbance. Since we cannot be certain about the reason for these major differences in microbial function at landscape scale, we suggest that future studies should investigate the role of biotic, abiotic, and stochastic factors in determining biocrust functionality in landscapes.

Future changes to precipitation and increased temperatures will reduce soil moisture across much of the Australian interior, as well as in drylands worldwide. This is likely to leave cyanobacterial biocrusts in a carbon-deficit (Strong et al., 2013), as cellular damage increases but the opportunities for cellular repair and carbon fixation are diminished. As a result, biocrusts may experience a decline in biomass, structure, and function which could have significant repercussions, by reducing the many ecosystem services they provide. For example, at Diamantina National Park, reduced dune biocrust cover is likely to result in greater wind transport of sand particles, which in turn act as a saltation mechanism on the claypans, increasing the magnitude and frequency of dust storm events. This will have implications for numerous characteristics of the dryland surface, including biocrust cover, potentially over vast areas, including albedo and heat balance, water and nutrient cycles (Rutherford et al, 2017). In areas where biocrusts are naturally dominated by cyanobacteria, climate changes may also favour species able to produce pigments to protect them from UV radiation (Couradeau et al., 2016, Williams et al., 2014) thus also altering the colour of the surface and ultimately albedo and heat balance (Rutherford et al., 2017).

5. Conclusions

We ran field experiments to determine the effects of biocrusts, light, temperature and moisture on soil CO_2 flux and photosynthetic activity on two dunes in Diamantina National Park in western Queensland, Australia. The findings demonstrate that biocrusts are a critical component of the dryland carbon cycle and that they are highly spatially variable at the landscape and at the small scale. The presence of biocrusts leads to a much stronger respiration response to hydration and to large CO_2 flux. Direct measurements in the field and laboratory also confirm that hydration is the critical factor for initiating and sustaining biocrust photosynthesis. Shaded conditions also favour photosynthetic efficiency. One of the most intriguing findings was that on one dune, despite the healthy biocrust cover and strong respiration response to hydration, we did not detect any photosynthetic activity by the fluorescence quantum yield technique. However, net carbon sequestration was occasionally observed and therefore we presume that photosynthesis was occurring but for some reason not detectable by the fluorimetry approach. This could be related to the microbial community composition, physical structure of biocrusts, or pigments in the biocrusts. What is clear is that conditions that favour biocrust respiration may not necessarily lead to biocrust photosynthesis. The findings suggest that a reduction in the moisture availability, fewer rainfall events and thus less cloud cover, together with higher temperatures, may impair the ability of biocrusts to carry out effective photosynthesis. Any climatic or land use changes that reduce the diversity of biocrust organisms will negatively impact the carbon cycle in Diamantina. It is therefore imperative to further our understanding of the interlinked processes of respiration and photosynthesis and their response to environmental change, to help ensure we manage drylands to optimise the numerous ecosystem services soil biocrusts provide.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

Andrew Thomas was supported by an Aberystwyth University Research Fund grant and an Australian Bicentennial Fellowship award from Kings College London. Joanna Bullard was supported by NERC

Grant NE/K011464/1. We thank Grant McTainsh and Helene Aubault for assistance in the field. The original version of this manuscript was significantly improved after careful reviews by Eva Stricker, Matthew Bowker (as editor) and an anonymous reviewer. The authors are very grateful for their time and constructive criticism, which have improved our paper.

References

Adir, N., Zer, H., Shochat, S., Ohad, I., 2003. Photoinhibition–a historical perspective. Photosynth. Res. 76 (1–3), 343–370.

Bates, B.C., Kundzewicz, Z.W., Wu, S. and Palutikof, J.P., Eds., 2008. Climate Change and Water. Technical Paper, International Panel on Climate Change (IPCC) Secretariat, Geneva.

Belnap, J., 2003. The world at your feet: desert biological soil crusts. Front. Ecol. Environ. 1 (4), 181–189. https://doi.org/10.1890/1540-9295(2003)001[0181:TWAYFD]2.0.CO;2.

Belnap, J., Weber, B., Büdel, B., 2016. Biocrusts as an organizing principle in drylands. In: Weber, B., Büdel, B., Belnap, J. (Eds.), Biological soil crusts: an organizing principle in drylands. Springer, Berlin, pp. 3–14.

Berkeley, A., Thomas, A.D., Dougill, A.J., 2005. Cyanobacterial soil crusts and woody shrub canopies in Kalahari rangelands. Afr. J. Ecol. 43 (2), 137–145.

Birch, H.F., 1964. Mineralisation of plant nitrogen following alternate wet and dry conditions. Plant Soil 20 (1), 43–49.

Büdel, B., Williams, W.J., Reichenberger, H., 2018. Annual net primary productivity of a cyanobacteria-dominated biological soil crust in the Gulf Savannah, Queensland, Australia, Biogeosciences, 15, 491–505. doi.org/10.5194/bg-15-491-2018, 2018.

Bullard, J.E., Mctainsh, G.H., Martin, P., 2007. Establishing Stage-Discharge Relationships in Multiple-Channelled, Ephemeral Rivers: a Case Study of the Diamantina River, Australia. Geogr. Res. 45 (3), 233–245. https://doi.org/10.1111/ages.2007.45.issue-310.1111/j.1745-5871.2007.00457.x.

Bullard, J.E., Ockelford, A., Strong, C.L., Aubault, H., 2018. Impact of multi-day rainfall events on surface roughness and physical crusting of very fine soils. Geoderma 313, 181–192.

Castillo-Monroy, A.P., Maestre, F.T., Rey, A., Soliveres, S., García-Palacios, P., 2011. Biological soil crust microsites are the main contributor to soil respiration in a semiarid ecosystem. Ecosystems 14 (5), 835–847.

Chappell, A., Strong, C., McTainsh, G., Leys, J., 2007. Detecting induced in situ erodibility of a dust-producing playa in Australia using a bi-directional soil spectral reflectance model. Remote Sens. Environ. 106 (4), 508–524.

Coe, K.K., Belnap, J., Sparks, J.P., 2012. Precipitation-driven carbon balance controls survivorship of desert biocrust mosses. Ecology 93 (7), 1626–1636.

Costelloe, J.F., Grayson, R.B., Argent, R.M., McMahon, T.A., 2003. Modelling the flow regime of an arid zone floodplain river, Diamantina River, Australia. *Environ. Model. Softw.* 18 (8-9), 693–703.

Couradeau, E., Karaoz, U., Lim, H., Nunes da Rocha, U., Northen, T., Brodie, E., Garcia-Pichel, F., 2016. Bacteria increase arid-land soil surface temperature through the production of sunscreens. Nat. Commun. 7, 10373.

Cowan, T., Purich, A., Perkins, S., Pezza, A., Boschat, G., Sadler, K., 2014. More frequent, longer, and hotter heat waves for Australia in the twenty-first century. J. Clim. 27 (15), 5851–5871.

Dettweiler-Robinson, E., Nuanez, M., Litvak, M.E., 2018. Biocrust contribution to ecosystem carbon fluxes varies along an elevational gradient. Ecosphere 9 (6), e02315. https://doi.org/10.1002/ecs2.2315.

Elliott, D.R., Thomas, A.D., Strong, C.L., Bullard, J., 2019. Surface stability in drylands is influenced by dispersal strategy of soil bacteria. J. Geophys. Res. Biogeosci. 124 (11), 3403–3418. https://doi.org/10.1029/2018JG004932.

Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M.O., Pöschl, U., 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. Nat. Geosci. 5 (7), 459–462.

Felde, V.J.M.N.L., Drahorad, S.L., Felix-Henningsen, P., Hoon, S.R., 2018. Ongoing oversanding induces biological soil crust layering—A new approach for biological soil crust structure elucidation determined from high resolution penetration resistance data. Geoderma 313, 250–264.

Ferrenberg, S., Tucker, C.L., Reed, S.C., 2017. Biological soil crusts: diminutive communities of potential global importance. Front. Ecol. Environ. 15 (3), 160–167. https://doi.org/10.1002/fee.2017.15.issue-310.1002/fee.1469.

FluorPen FP 100 series Operation Manual. www.psi.cz.

Fierer, N., Schimel, J.P., 2002. Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. Soil Biol. Biochem. 34 (6), 777–787.

Garcia-Pichel, F., Belnap, J., 1996. Microenvironments and microscale productivity of cyanobacterial desert crusts. J. Phycol. 32 (5), 774–782.

Grote, E.E., Belnap, J., Housman, D.C., Sparks, J.P., 2010. Carbon exchange in biological soil crust communities under differential temperatures and soil water contents: implications for global change. Glob. Change Biol. 16, 2763–2774. https://doi.org/10.1111/j.1365-2486.2010.02201.x.

Harel, Y., Ohad, I., Kaplan, A., 2004. Activation of Photosynthesis and Resistance to Photoinhibition in Cyanobacteria within Biological Desert Crust. Plant Physiology, 136 (2) 3070-3079; 10.1104/pp.104.047712.

Hu, C., Zhang, D., Huang, Z., Liu, Y., 2003. The vertical microdistribution of cyanobacteria and green algae within desert crusts and the development of the algal crusts. Plant Soil 257 (1), 97–111.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54 (2), 187–211.

Huang, J., Yu, H., Guan, X., Wang, G., Guo, R., 2016. Accelerated dryland expansion under climate change. Nat. Clim. Change 6 (2), 166–171. https://doi.org/10.1038/nclimate2837.

IPCC, 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, 688 pp.

Johnson, S.L., Kuske, C.R., Carney, T.D., Housman, D.C., Gallegos-Graves, L.V., Belnap, J., 2012. Increased temperature and altered summer precipitation have differential effects on biological soil crusts in a dryland ecosystem. Glob. Change Biol. 18 (8), 2583–2593.

Kieft, T.L., soroker, E., firestone, M.K., 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biol. Biochem. 19 (2), 119–126.

Kranner, I., Birtić, S., 2005. A modulating role for antioxidants in desiccation tolerance. Integr. Comp. Biol. 45 (5), 734–740.

Kutzbach, L., Schneider, J., Sachs, T., Giebels, M., Nykänen, H., Shurpali, N.J., Martikainen, P.J., Alm, J., Wilmking, M., 2007. CO_2 flux determination by closed-chamber methods can be seriously biased by inappropriate application of linear regression. Biogeosciences 4, 2279–2328.

Lan, S., Thomas, A.D., Tooth, S., Wu, L., Hu, C., 2019. Small-scale spatial heterogeneity of photosynthetic fluorescence associated with biological soil crust succession. Microb. Ecol. 78, 936–948. https://doi.org/10.1007/s00248-019-01356-0.

Lan, S., Wu, L.i., Zhang, D., Hu, C., 2012. Successional stages of biological soil crusts and their microstructure variability in Shapotou region (China). Environ. Earth Sci. 65 (1), 77–88.

Lan, S., Wu, L., Zhang, D., Hu, C., 2014. Desiccation provides photosynthetic protection for crust cyanobacteria Microcoleus vaginatus from high temperature. Physiol. Plantarum 152 (2), 345–354.

Lane, R.W., Menon, M., McQuaid, J.B., Adams, D.G., Thomas, A.D., Hoon, S.R., Dougill, A.J., 2013. Laboratory analysis of the effects of elevated atmospheric carbon dioxide on respiration in biological soil crusts. J. Arid Environ. 98, 52–59.

Lange, O.L., Meyer, A., Budel, B., 1994. Net photosynthesis activation of a desiccated cyano-bacterium without liquid water in high air humidity alone. Experiments with *Microcoleus sociatus* isolated from a desert soil crust. Funct. Ecol. 8 (1), 52. https://doi.org/10.2307/2390111.

Lembrechts, J.J., Aalto, J., Ashcroft, M.B., et al., 2020. SoilTemp: A global database of near-surface temperature. Glob. Change Biol. 26, 6616–6629. https://doi.org/10.1111/gcb.15123.

Ludwig, J.A., Wilcox, B.P., Breshears, D.D., Tongway, D.J., Imeson, A.C., 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. Ecology 86 (2), 288–297.

Maestre, F.T., Escolar, C., de Guevara, M.L., Quero, J.L., Lázaro, R., Delgado-Baquerizo, M., Ochoa, V., Berdugo, M., Gozalo, B., Gallardo, A., 2013. Changes in biocrust cover drive carbon cycle responses to climate change in drylands. Glob. Change Biol. 19 (12), 3835–3847.

Maroulis, J.C., Nanson, G.C., Price, D.M., Pietsch, T., 2007. Aeolian–fluvial interaction and climate change: source-bordering dune development over the past~ 100ka on Cooper Creek, central Australia. Quat. Sci. Rev. 26 (3-4), 386–404.

McTainsh, G., Strong, C., 2007. The role of aeolian dust in ecosystems. Geomorphology 89 (1-2), 39–54.

Miller, A., Schimel, J., Meixner, T., Sickman, J., Melack, J., 2005. Episodic rewetting enhances carbon and nitrogen release from chaparral soils. Soil Biol. Biochem. 37 (12), 2195–2204.

Miltner, A., Kopinke, F.-D., Kindler, R., Selesi, D., Hartmann, A., Kästner, M., 2005. Non-phototrophic CO_2 fixation by soil microorganisms. Plant Soil 269 (1-2), 193–203. https://doi.org/10.1007/s11104-004-0483-1.

Misra, A.N., Misra, M., Singh, R., 2012. Chlorophyll fluorescence in plant biology. INTECH Open Access Publisher.

Nanson, G.C., Knighton, A.D., 1996. Anabranching Rivers: their cause, character and classification. Earth Surf. Proc. Land. 21 (3), 217–239.

Placella, S.A., Brodie, E.L., Firestone, M.K., 2012. Rainfall-induced carbon dioxide pulses result from sequential resuscitation of phylogenetically clustered microbial groups. Proc. Natl. Acad. Sci. 109 (27), 10931–10936. https://doi.org/10.1073/pnas.1204306109.

Pringault, O., Garcia-Pichel, F., 2004. Hydrotaxis of cyanobacteria in desert crusts. Microb. Ecol. 47, 366–373.

Ravi, S., D'Odorico, P., Breshears, D.D., Field, J.P., Goudie, A.S., Huxman, T.E., Li, J., Okin, G.S., Swap, R.J., Thomas, A.D., Van Pelt, S., Whicker, J.J. and Zobeck, T.M., 2011. Aeolian processes and the biosphere. Reviews of Geophysics, 49, RG3001 10.1029/2010RG000328.

Rutherford, W., Painter, T., Ferrenberg, S. Belnap, J., Okin, G.D., Flagg, C. and Reed, S. C., 2017. Albedo feedbacks to future climate via climate change impacts on dryland biocrusts. Scientific Reports, 7, 44188 (2017). 10.1038/srep44188.

Šantrůčková, H., Bird, M.I., Elhottová, D., Novák, J., Picek, T., Šimek, M., Tykva, R., 2005. Heterotrophic Fixation of CO_2 in Soil. Microb. Ecol. 49 (2), 218–225. https://doi.org/10.1007/s00248-004-0164-x.

Slate, M.L., Sullivan, B.W., Callaway, R.M., et al., 2019. Desiccation and rehydration of mosses greatly increases resource fluxes that alter soil carbon and nitrogen cycling. Journal of Ecology 107, 1767–1778. https://doi.org/10.1111/1365-2745.13162.

Strauss, S.L., Day, T.A., Garcia-Pichel, F., 2012. Nitrogen cycling in desert biological soil crusts across biogeographic regions in the Southwestern United States. Biogeochemistry 108 (1-3), 171–182.

Strong, C.L., Bullard, J.E., Burford, M.A., McTainsh, G.H., 2013. Response of cyanobacterial soil crusts to moisture and nutrient availability. Catena 109, 195–202.

Tamm, A., Caesar, J., Kunz, N., Colesie, C., Reichenberger, H., Weber, B., 2018. Ecophysiological properties of three biological soil crust types and their photoautotrophs from the Succulent Karoo, South Africa. Plant Soil 429 (1-2), 127–146. https://doi.org/10.1007/s11104-018-3635-4.

Thomas, A.D., 2012. Impact of grazing intensity on seasonal variations in soil organic carbon and soil CO_2 efflux in two semiarid grasslands in southern Botswana. Philos. Trans. R. Soc. London B: Biological Sciences 367 (1606), 3076–3086.

Thomas, A.D., Dougill, A.J., 2006. Distribution and characteristics of cyanobacterial soil crusts in the Molopo Basin, southern Africa. J. Arid Environ. 64, 270–283.

Thomas, A.D., Hoon, S.R., 2010. Carbon dioxide fluxes from biologically-crusted Kalahari Sands after simulated wetting. J. Arid Environ. 74 (1), 131–139.

Thomas, A.D., Elliott, D.R., Dougill, A.J., Stringer, L.C., Hoon, S.R., Sen, R., 2018. The influence of trees, shrubs & grasses on micro-climate, soil C, N and CO_2 efflux: Potential implications of shrub encroachment for Kalahari rangelands. Land Degrad. Dev. 29 (5), 1306–13161.

Tracy, C.R., Streten-Joyce, C., Dalton, R., Nussear, K.E., Gibb, K.S., Christian, K.A., 2010. Microclimate and limits to photosynthesis in a diverse community of hypolithic cyanobacteria in northern Australia. Environ. Microbiol. 12, 592–607. https://doi.org/10.1111/j.1462-2920.2009.02098.x.

Viles, H.A., 2008. Understanding dryland landscape dynamics: do biological crusts hold the key? Geography Compass 2 (3), 899–919.

Wertin, T.M., Phillips, S.L., Reed, S.C., Belnap, J., 2012. Elevated CO_2 did not mitigate the effect of a short-term drought on biological soil crusts. Biol. Fertil. Soils 48 (7), 797–805.

Williams, W.J., Büdel, B., Reichenberger, H., Rose, N., 2014. Cyanobacteria in the Australian northern savannah detect the difference between intermittent dry season and wet season rain. Biodivers. Conserv. 23 (7), 1827–1844.